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FOSSIL VERTEBRATES
AND THE LATE PALAEOZOIC RED BEDS OF
PRINCE EDWARD ISLAND

By

Wann Langston, Jr.

DEPARTMENT OF NORTHERN AFFAIRS AND NATIONAL RESOURCES
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Issued under the authority of
The Honourable Walter Dinsdale, P.C., M. P.
Minister of Northern Affairs and National Resources

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By
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CONTENTS

	PAGE
Introduction.....	1
Palaeontological exploration.....	2
Occurrence of fossil vertebrates.....	2
Systematic descriptions.....	6
<i>Xenacanthus</i> near <i>X. texensis</i> (Cope) and <i>X. compressus</i> (Newberry).....	7
Family LEPIDOSIRENIDAE, <i>incertae sedis</i>	8
<i>Eryops megacephalus</i> Cope.....	9
Genus near <i>Eobrachyops</i> Watson.....	9
<i>Seymouria</i> Broili.....	12
Family DIADECTIDAE, genus and species indeterminate.....	13
<i>Diadectes</i> Cope.....	14
OPHIACODONTIA, Family <i>incertae sedis</i> . Genus and species indeterminate.....	14
<i>Bathygnathus borealis</i> Leidy.....	17
Genus cf. <i>Mycterosaurus</i> Williston.....	21
<i>Trichasaurus</i> Williston.....	23
The age of the Prince Edward Island red beds.....	25
Early dating.....	25
Recent progress.....	27
The evidence of fossil vertebrates.....	27
Some implications and inferences.....	29
Résumé.....	33
Addendum.....	34
References.....	35

Illustrations

	PAGE
PLATE I. Above: Permo-Carboniferous red beds exposed in a sea cliff at Crown Point, P.E.I. Below: Presumed dipnoan burrow exposed in sea cliff near Gallows Point.....	11
II. <i>Bathygnathus borealis</i> Leidy, holotype.....	18
FIGURE 1. Map of Prince Edward Island.....	5
2. <i>Xenacanthus</i> near <i>X. texensis</i> (Cope) and <i>X. compressus</i> (Newberry). Tooth.....	8
3. (A) <i>Seymouria</i> sp. Right femur.....	13
(B) DIADECTIDAE, genus and species indeterminate. Fragment of left dentary.....	13
4. OPHIACODONTIA, genus and species indeterminate. Left pterygoid.....	15
5. <i>Bathygnathus borealis</i> Leidy compared with <i>Dimetrodon limbatus</i>	20
6. Genus cf. <i>Mycterosaurus</i> Williston. Left dentary.....	21
7. <i>Trichasaurus</i> sp. Right metatarsal I.....	24

FOSSIL VERTEBRATES AND THE LATE PALAEOZOIC RED BEDS OF PRINCE EDWARD ISLAND

INTRODUCTION

The earliest published report of fossils in the red beds of Prince Edward Island appeared in a discursive letter by J. W. Dawson printed in the August 23 issue of the Royal Gazette of Charlottetown for 1842, and signed simply "D." In a "day or two" this giant among nineteenth century geologists explored much of the shore between De Sable and Orwell Bay and discovered most of the places where fossil plants are presently known to occur in that part of the Island. It is a mark of Dawson's genius that in his earliest work he drew many conclusions about the structure, stratigraphy, and origin of the red beds on Prince Edward Island that have not been effectively challenged to this day. And it will appear from what follows that his efforts at dating the rocks were not very wide of the mark.

It was early evident that stratigraphic studies on Prince Edward Island would not be easy, owing mainly to the virtual absence of fossils. Occasional plant remains provided the principal basis for conclusions, but their time-stratigraphic and ecological meaning even now may be subject to argument among palaeontologists. Matters became complicated in 1854 when Leidy erroneously inferred a Triassic age for the only known vertebrate fossil, *Bathygnathus borealis*. Although vertebrate palaeontologists later recognized Leidy's error and correctly identified *Bathygnathus* as a Permian pelycosaur, the time-stratigraphic picture has remained unclear in the geological literature of Prince Edward Island.

Recently, renewed geological activity on Prince Edward Island has revived interest in the age and origin of the red beds. Occasional discoveries of bone fragments by field geologists suggested that interesting fossil vertebrates might yet be found despite the virtual absence of any important discovery for over a century.

In 1960 and 1961 I spent about three months in a palaeontological reconnaissance of the Prince Edward Island red beds. Results, though not spectacular, have provided a better basis for dating the rocks than was hitherto available. For a really satisfactory understanding of the vertebrate fauna, much more collecting will be required. However, in view of the active geological investigations now under way in the province, it seems appropriate to offer some account of the palaeontological results so far obtained.

I should like to express my gratitude to Mr. B. Graham Rogers, Geological Officer of Prince Edward Island, for his co-operation and hospitality during the course of the work. My association in the field with Dr. Larry Frankel of the University of Connecticut and the Geological Survey of Canada was stimulating and informative—to Dr. Frankel goes credit for the discovery of the best preserved vertebrate fossil obtained in Prince Edward Island since the finding of Leidy's *Bathygnathus* specimen. For helpful discussions I am indebted to Dr. V. K. Prest, who is supervising the work of the Geological Survey of Canada on Prince Edward Island. Dr. Rainer Zangerl and Dr. E. C. Olson of Chicago are to be thanked, the former for the use of specimens at the Chicago Natural History Museum, the latter for reading the manuscript and giving helpful suggestions.

Dr. Horace G. Richards very kindly loaned me the type specimen of *Bathygnathus borealis* from the collections of the Academy of Natural Science of Philadelphia. Dr. Peter Hacquebard and Mr. S. Barss of the Geological Survey of Canada have been very helpful in discussing palynological data recently obtained from well cuttings on Prince Edward Island.

PALAEONTOLOGICAL EXPLORATION

Contrary to some published statements, fossils are not common in the Prince Edward Island red beds. Except for occasional explorations by palaeobotanical collectors, there has been little systematic search for palaeontological material since the earliest days. Plant fossils were the first organic remains reported (Dawson, 1842). Additional material is recorded by Dawson (1855), Dawson and Harrington (1871), Bain (1881), Bain and Dawson (1885), Holden (1913), and Darrah (1936). Prest (1961) notes recent discoveries of microfossils in well samples. Re-examination of existing collections and continued systematic search for new material are much needed.

Fossil invertebrates are practically unknown. Copeland (1957) reports an ostracod, *Carbonita inflata*, from a freshwater limestone near Little Miminegash Pond on the western side of the Island. Fragments in well cuttings from Governor Island are probably of invertebrate origin. Sinuous markings seen occasionally on bedding surfaces, especially in sandstones, may be trails of invertebrates (? gastropods), and clay-filled tubes in sandstones and limestones may be burrows. Most of these, however, are probably root-fillings. Dawson (1854) attributes vermicular holes in coniferous wood from south shore localities to activities of "Teredines or xylophagous larvae." Otherwise the entire section of red beds seems barren of invertebrate fossils.

The early discovery of the *Bathygnathus* specimen near New London was fortuitous. More than fifty years elapsed before another bone was found, by Case, during a brief tour of the south shore in 1915. Romer visited the Island in 1939, but his explorations along the coasts eastward from Charlottetown and between New London Harbour and the National Park were unrewarding (Romer, pers. comm.).

Occasionally in recent years geologists of the Geological Survey of Canada have encountered indeterminate fragments of bones at various places. My own work was largely confined to about the central third of Prince Edward Island, between Malpeque Bay and Montague. In this area all inland exposures of bedrock, as well as the accessible coastal outcrops, were examined. Thus approximately two-thirds of the outcrops that can be reached by foot on Prince Edward Island have been subjected to thorough exploration. To date, some twenty vertebrate specimens have been collected, of which no more than twelve have proved useful in this study.

OCCURRENCE OF FOSSIL VERTEBRATES

The type specimen of *Bathygnathus borealis* Leidy was discovered during the digging of a well, probably in 1845.¹ Although the well has long since been filled in, its location has been determined precisely by Dr. V. K. Prest of the Geological Survey of Canada. It was situated in a field 1.75 miles south of Cape Tryon Light in what is known as the French

¹ The exact date is not recorded, but B. Graham Rogers (pers. comm.) states that descendants of the finder, one Donald McLeod of French River, believe the discovery occurred in 1845. Dawson mentions the year 1852 opposite "*Bathygnathus*" in a fossil list appended to the 1855 edition of *Acadian Geology*, but this is probably the year the specimen came to Dawson's attention.

River District (Malpeque sheet-11 L/12-east half.¹ According to Leidy (1854b) the fossil came from a total depth of 21 feet, 9 inches, beneath the surface, and at a horizon 9 feet below the top of a "red sandstone with calcareous cement." The matrix beneath the specimen, however, contains large, irregular, tabular pieces of brick-red shale embedded in a sandstone matrix. This is one of the many clay breccias referred to in this report. The rock rapidly becomes more sandy toward the fossil, which evidently occurred at one of the sudden lithological transitions that characterize much of the Prince Edward Island red beds.

Case (1915a) reported finding the proximal end of a small sphenacodont humerus in conglomerate at Cape Traverse southeast of Borden, but no further information on this specimen is available. Presumed bone chips have been recovered twice (1908 and 1926) from well cuttings on Governor Island at depths of 1,459 and 180 feet, respectively.² The specimens have been turned over to me by Dr. A. S. Romer. They appear to be of invertebrate origin but are otherwise indeterminate.

Vertebrate fossils have also been collected at the following localities (Figure 1):

- P-5410. Keppoch Beach; immediately west of Keppoch Beach, between Keppoch and Battery Point, at entrance to Charlottetown Harbour.
- P-6001. Large excavation (locally termed "borrow pits"), 0.8 miles south of Highway No. 3 and 1.5 miles northwest of Seatrout Point, Charlottetown sheet (11 L/3), east half.
- P-6002. Base of sea cliff 0.6 miles south of locality P-6001, Charlottetown sheet (11 L/3), east half.
- P-6003. Crown Point; 5.4 miles southeast of the eastern approach to Charlottetown - Hillsborough River bridge, Charlottetown sheet (11 L/3), east half.
- P-6004. Squaw Point; 0.5 miles south of Highway No. 3 and 3.3 miles southeast of the east end of Charlottetown - Hillsborough River bridge, Charlottetown sheet (11 L/3), east half.
- P-6005. Haszard Point; 1.6 miles south of Highway No. 3 and No. 5 interchange and 3.0 miles southeast of east end of Charlottetown - Hillsborough River bridge, Charlottetown sheet (11 L/3), east half.
- P-6006. Gallows Point locality No. 1; near base of eastern sea cliff about 0.15 miles from tip of Gallows Point (Galla's Point of old reports), Montague sheet (11 L/2), west half.
- P-6007. Gallows Point locality No. 2; 0.55 miles north-northeast of Gallows Point, Montague sheet (11 L/2), west half.
- P-6008. Selkirk Park locality No. 1; near base of low steep sea cliff about 50 yards north of the bathing landing, 0.5 miles northwest of Selkirk Road and highway No. 4, Montague sheet (11 L/2), west half.
- P-6009. Selkirk Park locality No. 2; about 50 yards east of locality P-6008, Montague sheet (11 L/2), west half.
- P-6106. Rocky Point; at base of sea cliff on south side of point, 2.3 miles northeast of tip of Rice Point and 1.4 miles west-southwest of Bacon Point, Charlottetown sheet (11 L/3), east half.
- P-6107. Hog Island; below lighthouse at southeast tip of island, Malpeque sheet (11 L/12), east half.
- P-6108. Spring Valley; in an excavation (borrow pit) on north side of Spring Valley - Darnley road, 1.75 miles north of Spring Valley and 0.6 miles south-southwest of Darnley, just north of the bend where the road turns from north to west, Malpeque sheet (11 L/12), east half.
- P-6109. Lobster Point; a few feet above beach in sea cliff, 1.05 miles east of Seatrout Point and 2.0 miles west of Haszard Point lighthouse on south coast of Keppoch Peninsula, Charlottetown sheet (11 L/3), east half.
- P-6110. In sea cliff at beach level just east of Gallows Point, 0.5 miles north-northwest of Orwell Point and 0.2 miles north-northeast of tip of Gallows Point, Montague sheet (11 L/2), west half.

¹ Map citations in this section refer to sheets of the *Canada, National Topographic Series* (1:50,000).

² Imperial Oil Company Governor Island wells Nos. 1 and 2.

P-6111. Irishtown; in excavation (borrow pit) south side of Highway 7-A, 0.9 miles south-southeast of Sea View and 0.77 miles north-northwest of Park Corner, about 2.4 miles north of Irishtown, Malpeque sheet (11 L/12), east half.

P-6112. Seacow Head; in sea cliff on west side of Richmond Cove, 0.5 miles east of Seacow Head lighthouse and 1.7 miles south-southeast of Graham Head, Summerside sheet (11 L/5), west half.

Poorly preserved pieces of bone have been noted in the field at a number of other localities but were not collected. They occurred mostly near the localities listed above and add nothing to information available there.

Most of the fossils found *in situ* were exposed in sea cliffs. However, at Crown Point (P-6003), Haszard Point (P-6005), Gallows Point No. 2 (P-6007), Selkirk Park No. 1 (P-6008), and Hog Island (P-6107), specimens were obtained from scattered boulders on the beaches. These seem to have been derived locally by wave action against sea cliffs, but some transportation by ice rafting may have occurred, especially at Hog Island. At McDonald's borrow pit (P-6001), Spring Valley (P-6108), and Irishtown (P-6111), bones were found in heavy boulders left in the quarries by excavators.

Most vertebrate fossils have been obtained from clay breccias and clay-gall conglomerates of intraformational character which occur repeatedly through the section, but which seem more abundant in the lower part. These are composed of sand and siltstone matrices containing varying amounts of red clay and shale particles. The pellets vary from very small, well-rounded pebbles to angular, tabular pieces measuring up to three inches in diameter. Size stratification in which larger pebbles generally occur beneath finer ones, is often apparent, and the transition between grades is often rapid. Large angular pieces sometimes comprise edgewise conglomerates and lack orientation, but most of the better-rounded fragments are arranged with their broad surfaces parallel to the bedding. In many instances, it is apparent that the clay pellets were derived from underlying strata.

Red clay, silt, and sandstone make up most of the remaining bedrock. Plant fossils are locally abundant in these lithologies, but few vertebrate remains have been found in them. At Haszard Point (P-6005) an amphibian premaxilla occurred in thin-bedded red sandstone which contained no clay fragments. The vertebrate-bearing matrix at Gallows Point No. 1 is a dark red-brown to chocolate coloured, soft gritty sandstone containing occasional red clay pebbles. One specimen was found at Lobster Point (P-6109) in soft red siltstone between two clay breccia strata.

Freshwater limestones are little developed on Prince Edward Island, and the two exposures I examined have yielded no vertebrate remains. Evaporite marls, dark-grey paludal deposits, marine limestones, coal, and underclay are unknown in surface exposures. Conglomerates of igneous and metamorphic pebbles have provided no fossils.

Along the coasts all exposures are subjected to rapid wave erosion—tides of six feet or more occur, and weathering surfaces are continuously renewed. Fossils thus exposed are rapidly destroyed, but a continuing supply is assured. Virtually no erosion occurs inland except on surfaces exposed by excavation activities.

With the exception of the type specimen of *Bathynathus borealis*, all fossil bones show evidence of some pre-burial transportation. Only a small pelycosaur metatarsal from the Spring Valley locality was completely intact when found, although xenacanth shark teeth from Gallows Point and Seacow Head may have been complete before

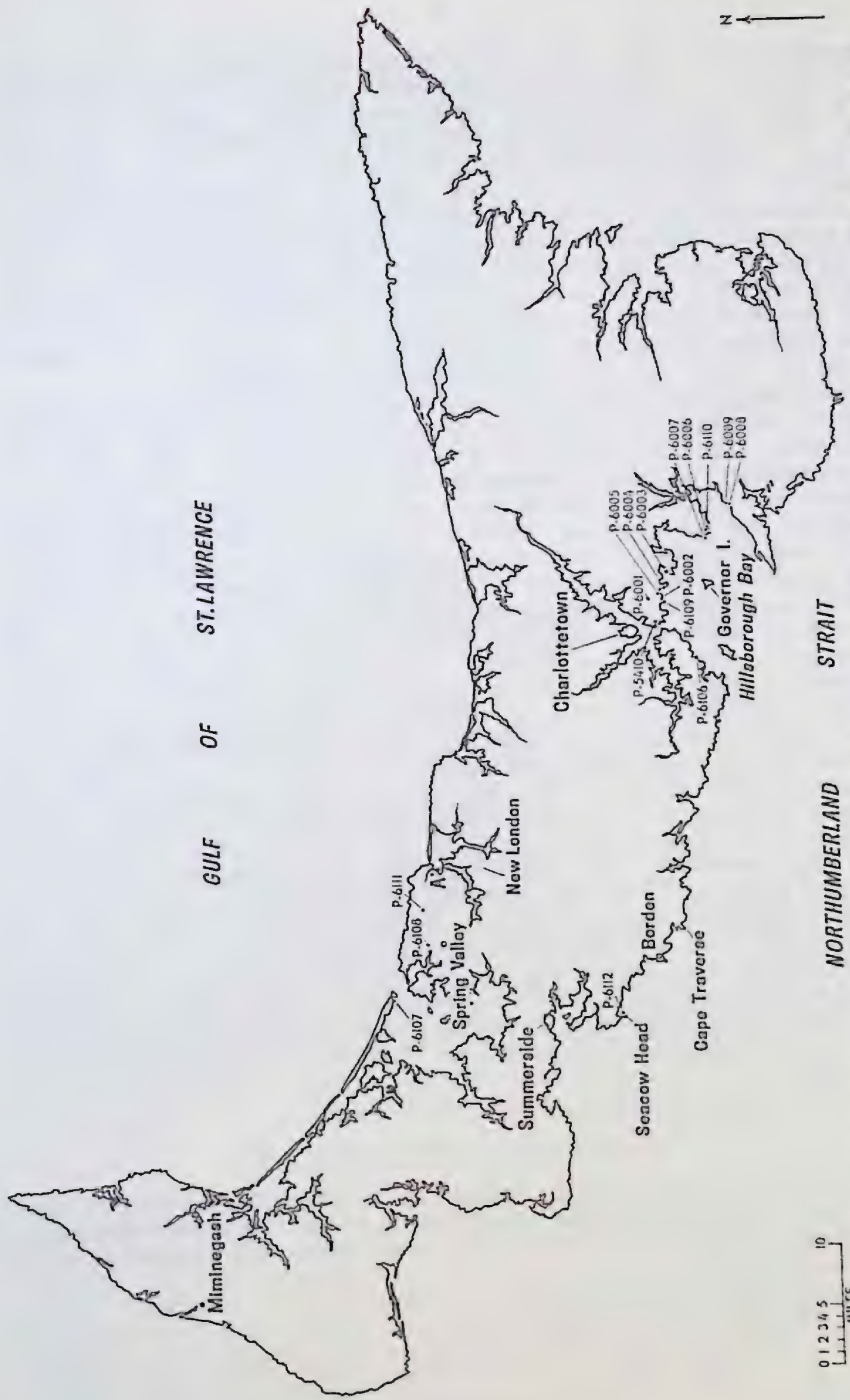


FIGURE 1. Map of Prince Edward Island. Vertebrate fossil localities are designated by numbers. A. approximate location of old well where the type of *Bathynathus borealis* Leidy was obtained.

exposure to the waves. The bones are generally abraded, and usually only the more compact parts are preserved. It is therefore surprising that most of the specimens in fairly coarse clastic matrices are small and often fragile elements. In some cases such structures apparently escaped destruction because they travelled with the fine sediments occupying voids between the large irregular pieces of claystone, or were more resistant or resilient than the brecciated bits of clay which may not have been lithified at the time of deposition. The slab of *Bathynathus* facial bones shows no pre-burial damage except separation from the rest of the skull. The specimen is large, broad, and flat with a smooth exterior and presumably irregular interior surface. It is just the kind of bone that becomes anchored on present-day beaches and escapes the damage to which rolling and water-tossed specimens are subject.

Although small unidentifiable scraps of bone are sometimes encountered near a more complete specimen, only at Spring Valley (P-6108) has close association of several bones been observed at one horizon. This occurrence is interesting because it provides the only evidence in one deposit of a variety of vertebrates. Several large indurated boulders of clay breccia contained the bones among which were found the only instance of retained articulations yet seen: a central segment of a snout and mandible of a small labyrinthodont and a metatarsal and phalanx of a pelycosaur. During preparation of these specimens it appeared that they must already have been contained in red clay prior to inclusion in the breccia. The amphibian jaws which were badly shattered were still held in proper apposition despite pre-burial loss of the articular segments, and tips of some mandibular teeth were embedded in red clay that filled the longitudinal groove medial to the maxillary tooth row. A phalanx tightly articulated with the metatarsal was incomplete distally, but the broken and somewhat worn stump of the bone was completely surrounded by clay breccia when found. Some other delicate bones associated with these specimens are almost complete but have no red shale adhering to them; they bear the impress of sand grains from the surrounding matrix on their external surfaces. They were evidently first buried in a red mud which became hardened, but perhaps not thoroughly lithified. This clay was subsequently torn up and incorporated in a clay breccia. (A stratum of large angular clay pellets immediately beneath the bone level implies rapid erosion, brief transportation, and quick burial.) A few of the bones were completely freed of surrounding clay before inclusion in the sandy matrix of the breccia. It is impossible to know if permineralization had commenced in the bones prior to final burial, but it can be assumed that the time required for these events was brief.

SYSTEMATIC DESCRIPTIONS

Since the stratigraphic interpretations to follow depend largely upon the correct identification and understanding of the few known and badly preserved fossils, these are described in some detail. The composite faunal list comprises—

Class CHONDRICHTHYES

Subclass ELASMOBRANCHII

Order XENACANTHODII

Family XENACANTHIDAE

Xenacanthus near *X. compressus* (Newberry) or
X. texensis (Cope)

Class **OSTEICHTHYES**Subclass *CHOANICHTHYES*

Order DIPNOI

Family LEPIDOSIRENIDAE, *incertae sedis*

Genus and species indeterminate

Class **AMPHIBIA**Subclass *APSIDOSPONDYLI*

Order TEMNOSPONDYLI

Suborder RACHITOMI

Family ERYOPIDAE

Eryops megacephalus Cope

Suborder STEREOSPONDYLI

Family BRACHYOPIDAE

Genus near *Eobrachyops* Watson

Suborder SEYMOURIAMORPHA

Family SEYMOURIIDAE

Seymouria BroiliClass **REPTILIA**Subclass *ANAPSIDA*

Order DIADECTOMORPHA

Family DIADECTIDAE

Genus and species indeterminate

Diadectes CopeSubclass *SYNAPSIDA*

Order PELYCOSAURIA

Suborder OPHIACODONTIA

Family *incertae sedis*

Genus and species indeterminate

Suborder SPHENACODONTIA

Family SPHENACODONTIDAE

Bathygnathus borealis Leidy

Suborder EDAPHOSAURIA

Family NITTOSAURIDAE

Genus cf. *Mycterosaurus* Williston

Family CASEIDAE

Trichasaurus Williston

These animals are from different horizons, but their stratigraphic occurrence is best discussed after the descriptions of the fossils.

Xenacanthus near *X. texensis* (Cope) and *X. compressus* (Newberry)

(Figure 2)

Two teeth of the familiar "*Diplodus*" form are referred here. There is no basis for distinguishing them from either of the species. One, NMC 9916, is from soft chocolate-brown granular sandstone at Gallows Point (P-6006). It is better preserved than the second tooth, NMC 9988, which consists largely of a natural mould in a piece of highly calcareous clay breccia from Seacow Head (P-6112). In addition, from Gallows Point (P-6007), there is a small spiral coprolite of the type usually attributed to xenacanth sharks (NMC 9917).

The teeth have one nearly straight cusp and a somewhat longer one that curves gently away from the first. The cusps apparently had ovate cross-sections, but whether the edges were sharp or crenulated cannot be



FIGURE 2. *Xenacanthus* near *X. texensis* (Cope) and *X. compressus* (Newberry). Tooth, NMC 9916, from Gallows Point (Loc. P-6006). Nat. size.

determined. The bases of the cusps meet in a sharp V, but it is impossible to say if intermediate cuspules were present since in both teeth the area that would have contained the cuspule has been split off. The lingual half of the base plate is preserved in No. 9916. It was apparently wider than long and triangular in basal plan. The edges are thick and rounded. There is a thick, but narrow apical button (see Hotton, 1952, for terminology used here). This is pierced on either side near the base by a small foramen. The basal plate and especially the apical button seem to stand more vertical in relation to the cusps than in a tooth of the Pennsylvanian *X. compressus* (Newberry) figured by Hotton (Fig. 2B), but this may be a post mortem effect.

There is no possibility of confusing these teeth with those of the geologically younger *X. platypternus* (Cope) which have a broad flattened base and backwardly-curved cusps.

Family LEPIDOSIRENIDAE, *incertae sedis*

(Plate I)

The lungfishes are evidently represented in the Prince Edward Island collections by the cast of a burrow, NMC 10016, found near Gallows Point (Locality P-6110).

The specimen is a slightly distorted columnar cylinder of soft grey sandstone about 28 cm high. The diameter at the top is about 10 cm, but at midheight the cross-section becomes broadly oval with a greatest diameter of 10 cm. At the base, the section becomes more circular again and diminishes to about 8 cm in diameter. The sides of the column are vertically striated, but whether as a result of animal activity or of deformation in the surrounding shale it is not clear. Upon excavation the cylinder broke into several discs whose separations correspond to bedding planes within the sandstone column but which seem independent of bedding in the bright red joint clay that surrounds the column. At several places, however, horizontal movement along the claystone bedding planes has carried through the column producing shear "bedding." At these places also the sandstone of the cylinder has been forced out along the bedding planes of the claystone, forming thin and narrow annulae around the column.

The top of the burrow is sharply truncated by a lenticular sandstone body which supplied the material filling the burrow. The sandstone of the lens is dark red; the grey colour of the cylinder results from reduction of red iron oxide by waters confined to the sand by the relatively impervious claystone surrounding it. At several places the grey reduced zones extended outward along bedding planes in the claystone. The base of the burrow was shallowly concave.

The cylinder was split in the laboratory, but no organic remains were found in it. However, so similar is it to undoubted dipnoan burrows from the Texas Permian (Romer and Olson, 1954) that I have no doubt that it originated in the same fashion. As in most of the burrows from Texas, the fish had vacated the burrow before it was filled with sand, and there is no way of knowing what genus was responsible for it. The burrows in Texas are thought to have been dug by a presumed lepidosirenid, *Gnathorhiza*.

Eryops megacephalus Cope

This ubiquitous amphibian is represented by a left premaxilla, NMC 9990, from Lobster Point (P-6109). The specimen though incomplete is well preserved. The missing parts were cast in plaster from impressions in the matrix. Remains of eleven marginal teeth and alveoli are visible; the median suture is preserved anteriorly; and, posteriorly, the beginning of the broad dorsal ridge that passes mesially to the nares in *Eryops* is well shown. The characteristic depression in front of the nares is also partly preserved. The sculpture is characteristically eryopid.

I have compared this bone with a suite of *E. megacephalus* skulls at Chicago and am unable to distinguish it from several of them. The specimen is in the lower part of the medium-size range for the adult individuals and agrees closely in every detail with a snout from the Arroyo formation at West Coffee Creek, Baylor County, Texas.

Genus near *Eobrachyops* Watson

From a clay breccia boulder at the Spring Valley locality (P-6108) come several fragments of labyrinthodont dermal bones, NMC 10012. It is not certain that these are derived from one individual, but their similarly small size and proximity of occurrence suggest that they at least belong to the same species.

The most informative specimen comprises a short section of opposing upper and lower jaws. These lay parallel to the bedding plane, and differential erosion along this plane had caused much damage to the specimen. The bones are also crushed. A thin layer of clay evidently surrounded the bones, and the nature of the fossil suggests that it may have been redeposited. The significance of this is discussed elsewhere.

Of the upper jaw we have a short section of the right maxilla which contains space for 20 teeth in a distance of 13.5 mm. Attached to this is a short section of right palatine bone. Little is seen of the maxilla except a narrowly exposed, roughly sculptured lateral edge, and its dentigerous surface. The latter has the form of a narrow flattened ridge bounded medially by a deep longitudinal sulcus (which still contains tips of mandibular teeth *in matrix*). The ridge carries a series of labyrinthine teeth, round in basal section and with large pulp cavities. Alveoli tend to have a quadrangular outline, and vacant alveoli alternate with functional teeth in fairly regular order.

The palatine is a shelf-like bone, incomplete behind, broken off in front, but seemingly intact along some of its medial edge. It was narrow posteriorly, but in the anterior part of the preserved section it expands medially and here supports two palatine tusks arranged one behind the other. In front of this it again contracts. There is a trace of a tongue-and-groove suture along the posteromedial edge, presumably for attachment of the palatal ramus of the pterygoid, but the disappearance of the suture anteriorly suggests that here the palatine entered the interpterygoid vacuity for a short distance. Another surface suggestive of a sutural contact occurs

PLATE I

ABOVE: Permo-Carboniferous red beds exposed in a sea cliff at Crown Point, P.E.I. The hammer marks a characteristically developed lens of clay breccia of the type that has yielded most of the vertebrate fossils. These beds are in the lower part of the section available on Prince Edward Island.

BELOW: Presumed dipnoan burrow exposed in sea cliff near Gallows Point. The cast of the interior of the burrow is filled with fine sandstone derived from the lens just above the red joint clay which the burrow penetrates.



on the medial edge opposite the space between the tusks. This probably contacted the vomer, thereby forming the posterior rim of the choana. Anterior to this and mesad to the anterior tusks, the bone is thickened dorsoventrally forming a low dorsal buttress and indicating that the facial region above was depressed. Remains of the edge of the choana are visible below the buttress. The palatine seems to extend anterolaterally between the choanal margin and the maxilla, but it is broken off short, in front of the anterior tusk.

The posterior tusk is represented by a large round crater, the anterior one by the broken base of a tooth which seems to have an anteroposteriorly ovate section. There is no evidence of a distinct basin containing this tusk pair or of any bony ridge surrounding it. Behind the posterior tusk there is a low longitudinal ridge which appears to contain the broken bases of a number of palatal teeth arranged in a single row.

Very little can be said of the dentary. The teeth were apparently similar to those above, and there is no evidence of coranoid denticles or teeth. There may have been some enlarged teeth anteriorly, but this is far from certain.

The features just described occur in various temnospondyles allied to *Trimerorhachis* but are not generally present in other pre-Triassic labyrinthodonts. The existence of a well-defined palatal tusk pair unaccompanied by a row of *relatively large* teeth behind tends to distinguish this animal from *Trimerorhachis*, although some *Trimerorhachis* approach the condition described here. The entry of the palatine into the interpterygoid vacuity, however, separates the Prince Edward Island animal from *Trimerorhachis* as now defined.

The early Permian brachyopid amphibian *Eobrachyops*, which Watson (1956) believed might have some connection with *Trimerorhachis*, seems to agree with the present species in all respects, except that no mention is made of any teeth other than palatal tusks in *Eobrachyops*. If my interpretation of the palatine from Prince Edward Island is correct, the bone may have contacted the vomer at the side of the choana in a way seen elsewhere in labyrinthodonts only in *Eobrachyops*. It is perhaps also significant that fragments accompanying this specimen—possibly squamosal and jugal—have a peculiar ridge and groove sculpture resembling that of *Eobrachyops*. It is entirely unlike the sculpture of *Trimerorhachis*.

The present specimens also suggest the Pennsylvanian (Linton) genus *Saurerpeton*. Although this animal is thought to have had only one palatine tusk instead of the usual pair, Romer (1948) suggests that there may have been additional teeth in the palate. In this regard the Prince Edward Island species might have resembled *Saurerpeton* more than *Eobrachyops*. If some connection exists between *Eobrachyops* and *Saurerpeton* the resemblances of the present animal to both of them are not surprising.

Eobrachyops is said to have come from Clear Fork rocks of Texas, but its exact occurrence is unknown.

Seymouria BROILI

(Figure 3A)

A small right femur, NMC 9989, from calcareous sandy clay-breccia in the New London district (Locality P-6111) is clearly seymouriamorph in form. Comparison with a well-preserved femur of *Seymouria baylorensis* leaves little doubt that the specimen from Prince Edward Island belonged to *Seymouria*.

The bone, having lost before burial the proximal end, most of the posterior condyle, and much of the ventral ridge system, is incomplete, but it is well preserved and provides a good basis for the accompanying reconstruction.

This was a short, heavy bone with deeply concave fore and aft edges and apparently greatly expanded ends. The shaft seems shorter and relatively more slender than in the *Seymouria* femur compared. The intertrochanteric fossa is relatively longer, the fourth trochanter is placed more distally, and the adductor ridge is therefore shorter than in *S. baylorensis*; the popliteal area is better defined than there.

These differences are not so great as those to be found between extreme conditions in a large number of *S. baylorensis* femora in collections at the Chicago Natural History Museum and illustrated in the literature. The bone, before reconstruction, showed a strong similarity to a femur assigned to *Desmospondylus anomalus* by Williston (1910, Pl. 16, Fig. 4). This "species" has long been recognized as juvenile *S. baylorensis*. The small size of the Prince Edward Island specimen and the general resemblance which it bears to the femur of *D. anomalus* suggest that it, too, belonged to an immature individual.

DIADECTIDAE, genus and species indeterminate

(Figure 3B)

A fragment of a left dentary bone of a small reptile, NMC 9918, is referable to the Diadectamorpha. It was found in a large boulder of calcareous sandy clay-breccia upon the beach at Selkirk Park, No. 1 (Locality P-6008). The source of the boulder was not determined, but it may have been derived from near-by exposures.



FIGURE 3. (A). *Seymouria* sp. Right femur, NMC 9989 from New London district (Loc. P-6111). Nat. size. Reconstruction based on femur of *S. baylorensis* (Chicago Nat. Hist. Mus. - U.C. 1313). (B). Diadectidae, genus and species indeterminate. Fragment of left dentary, NMC 9918, from Selkirk Park (Loc. P-6008). Above, oblique view from within; below, polished section of base showing implantation of teeth. Approx. X2 nat. size.

The specimen contains the truncated stalk-like roots of six teeth. These occupy a distance of only 10.5 mm. The greatest observed transverse diameter of the fragment (which is still partly embedded in matrix) is

about 5.0 mm. Of bone there is only a thin plate, which is bounded at either side by an elevated rim. Between rims there is a broad longitudinal trough containing the teeth. The roots are placed closer to one—presumably labial—side than to the other. No trace of dental crowns remains, but a matrix cast of the pulp cavity of one tooth is constricted near the top; it then expands again transversely suggesting that a broad crown of diadectid form was present. Furthermore the pulp spaces appear to have ended bluntly above as in *Diadectes*. The roots are closely spaced; on polishing the basal surface of the specimen, I found that the roots were in virtual contact with one another within the jaw bone. The roots are transversely oval in section, but the exposed part seems less quadrangular than usual in *Diadectes*. However, the polished bases of the roots show these to be sharply quadrangular. One root has an anteroposterior diameter of 2.0 mm, and a width of 3.0 mm. Its pulp cavity describes a "rounded" parallelogram with diameters of 1.0 and 2.2 mm, respectively. Vertical grooves that characterize roots of the molariform teeth of *Diadectes* are not apparent on the exposed surfaces of any of the roots, but the polished section shows that such grooves were present. At the middle of the series, grinding has also revealed part of a medially-placed alveolar pit adjacent to one of the roots. Such pits are characteristic of diadectids.

This specimen is too incomplete to permit certain generic assignment. It is far smaller than any *Diadectes* known to me, but it is a little larger than a similar fragment from Conemaugh deposits in Pennsylvania, provisionally assigned to *Desmatodon* by Romer (1952). The roots of the teeth seem more closely spaced than usual in *Diadectes*, and in section they are less quadrangular than usual, at least in the more posterior parts of the dental series. In these regards the roots may be more comparable to teeth of *Stephanospondylus* from the Middle Rotliegende of Germany (Geinitz and Deichmüller, 1882, Pl. IV, Fig. 2).

Romer (1952) suggested that the tiny Conemaugh jaw referred to above might pertain to a young *Desmatodon*, and the present specimen may well represent an immature diadectid of some sort.

Diadectes Cope

The above supposition is reinforced by the discovery only a few yards away (Locality P-6009) of a postzygapophysis, NMC 9919, of unmistakable diadectid form. The specimen is not large, but it came from an individual much larger than the possessor of the jaw fragment. The vertebra was well within the size range of the genus *Diadectes* and is indistinguishable from zygapophyses on dorsal vertebrae ascribed to *D. sideropelicus* from the Admiral formation in Texas.

OPHIACODONTIA, Family *incertae sedis*

Genus and species indeterminate

(Figure 4)

Assigned here is a left pterygoid and attached epipterygoid of a moderately small reptile, NMC 9914. The specimen was found in a boulder of clay-breccia on the beach at Squaw Point (Locality P-6004) and may have been derived from the adjacent low sea cliff. Though badly broken when found, it has been possible to reconstruct the specimen to virtual completeness; the distal half of the quadrate ramus of the pterygoid was preserved as an impression in matrix, the anterior end of the palatal ramus

was lost before burial, and the ventral edge of the transverse ramus was partly destroyed by weathering. The dorsal column of the epipterygoid, though damaged, is interpretable.



FIGURE 4. Ophiacodontia, genus and species indeterminate. Left pterygoid, NMC 9914, from Squaw Point (Loc. P-6004). Approx. nat. size.

The pterygoid comprises the usual three rami. As preserved, it is 39.0 mm long and has a greatest width at the transverse ramus of 24.0 mm. The quadrate ramus is 24.0 mm long. The well-developed basal process originates mostly anterior to the intersection of the three rami, but its most posterior part lies opposite the base of the transverse ramus. The process was removed during preparation revealing a thin hemicylindrical shell of bone, flooring a pocket which housed the basalar articulation of the epipterygoid. (The flange of the pterygoid may also have participated in the basicranial articulation in *Varanosaurus* fashion.) The transverse ramus is thickened where it provided a base for palatal denticles. How far it extended below the general level of the palate is uncertain owing to the difficulty of determining the exact orientation of the somewhat distorted pterygoid-epipterygoid complex. From its lowest point, laterally, the flange rises anteriorly and forms at the side a thickened coronoid buttress. The palatal ramus is broad and but little emarginated at its reflected median edge, indicating that the interpterygoid vacuity was long and narrow. There is no trace of a median suture. Two longitudinal ridges cross the palatal surface, one coinciding with the edge of the interpterygoid vacuity; the other, heavier one, diverging forward from its origin opposite the basal articular area. These ridges are separated by a deep sulcus, and the lateral ridge is bounded at the side by a broad saddle-shaped vault whose lateral edge is the coronoid buttress of the transverse ramus. Part of an overlapping sutural surface is preserved at the anterior end of this saddle-shaped area. This provided articulation with the ectopterygoid, but there is no trace of an attachment for the jugal. The quadrate ramus is slender and tapers to a point posteriorly. Anteriorly it thickens toward the base of the transverse ramus, but it lacks a strong ventral keel. The median edge expands in the anterior half of the ramus forming a thin flange which is slightly deflected and produces a longitudinal channel on the ventral surface of the bone.

A well-developed dentition occurs on the palatal ridges. A series of long conical teeth were present along the ventral edge of the transverse ramus. It is impossible to tell if there was more than one row of teeth, but a short distance in front and at a slightly higher level there is another

transverse but shorter series of about six teeth. This series divides laterally where at least two large teeth occur, side by side, at the edge of the coronoid buttress. There is even some evidence of at least one additional tooth anterior to these at the edge of the buttress. The longitudinal ridges of the palatal ramus are heavily denticulate. The teeth are smaller than some on the transverse ramus but are more numerous and are less regularly arranged. Denticles are most numerous on the lateral ridge. The bony base that supports them is thickened and bounded medially and posteriorly by a narrow groove. It is possible that some teeth on the medial ridge were arranged in a longitudinal series, but others were randomly placed. All pterygoid teeth were firmly attached to the bone, which in places rose to form shallow alveoli around the bases of teeth.

The epipterygoid is not completely visible. There is a long slender dorsal process which widens below to enclose a broad channel that passes lateral to the cupped area at the base of the pterygoid. Some pterygoid ossification exists deep within the cup, but a large void remains which was filled in life by persistent epipterygoid cartilage. Behind the cup the epipterygoid wedges narrowly into the base of the quadrate ramus of the pterygoid, but there is no sign of a quadrate process and no suggestion of an articulation with the quadrate (possibly this is hidden by matrix).

This specimen evidently pertains to the Pelycosauria. The central location of the basal articular process, the character of the transverse flange of the pterygoid, and the disposition of the teeth are suggestive of the Ophiacodontia.

The pterygoid-epterygoid complex of ophiacodonts is known mainly from *Ophiacodon* itself. In addition to resemblances noted above, the specimen agrees with *Ophiacodon* (and differs accordingly from sphenacodonts exemplified by *Dimetrodon*) in:

- (1) the straight (interpterygoid) edge of the palatal ramus of the pterygoid which resulted in a long narrow interpterygoid vacuity;
- (2) the low position of the basal articular process in relation to the palatal surface;
- (3) the absence of an interlocking union between pterygoid and quadrate;
- (4) the persistently cartilagenous basal part of the epipterygoid, which was supported from below by a hemicylindrical shelf of pterygoid;
- (5) the absence of a great thickening of the tooth-bearing part of the transverse flange of the pterygoid.

The pterygoid, however, is more heavily constructed than in *Ophiacodon*, and it may have been relatively short. The transverse flange is much broader in relation to the length of the quadrate ramus, suggesting the skull was wider and more compact than in *Ophiacodon* or *Varanosaurus*. The quadrate ramus lacks the well-developed flange which in *Ophiacodon* forms a floor for the middle ear cavity (Romer and Price, 1940), and there is no ventral keel of *Ophiacodon* character. Absence of a bony epipterygoid contact with the quadrate could be significant. Comparison with *Clepsydraps* is not possible, of course, since the pterygoid in this (presumed) *Ophiacodon* antecedent is not known.

Of particular interest are the differences between the pterygoid dentitions of this specimen and *Ophiacodon*. Although the basic pattern is the same, the number of teeth is much greater than in *Ophiacodon*, owing to a more random arrangement of the denticles. Correlated with this, the

tooth-bearing ridges seem almost pad-like and are much heavier than in *Ophiacodon*. They seem more comparable to the structure in the unrelated *Araucoscelis* and *Broomia*. Among pelycosaur, pterygoid dentitions are supported by pad-like bony bases only in the edaphosaurs and some caseids. *Edaphosaurus* has the most aberrant palatal dentition, and the transverse flange of the pterygoid is no longer distinguishable. *Casea* retains something of the flange but has a complete pavement of denticles on the pterygoid. However, the great caseid *Cotylorhynchus* had a less complete, more regularly arranged pterygoid dentition with a strong but not greatly deflected transverse flange. Teeth were apparently present along the coronoid edge of the pterygoid. The pterygoid dentition just described, though not approaching conditions in edaphosaurs, none the less suggests a trend in that direction and is somewhat suggestive of conditions in *Cotylorhynchus* (the presence of teeth at the coronoid edge of the pterygoid is a very unusual feature shared with *Cotylorhynchus*). Further comparisons reveal a resemblance to *Cotylorhynchus* in the shape of the quadrate ramus (see Romer and Price, 1940; pl. 19), and the inclined basal articular process of the pterygoid fits the description given by Romer and Price for *Edaphosaurus*. Moreover, absence of a quadrate-directed process of the epipterygoid, if confirmed, is a strong edaphosaurid characteristic.

Thus, although sufficient ophiacodont characters are present in this specimen to justify its assignment to the suborder, it is not referable to known genera, and it displays distinctive caseid and edaphosaur tendencies. Interesting as it is, the specimen is not sufficiently complete to furnish an adequate diagnosis and must therefore go unnamed.

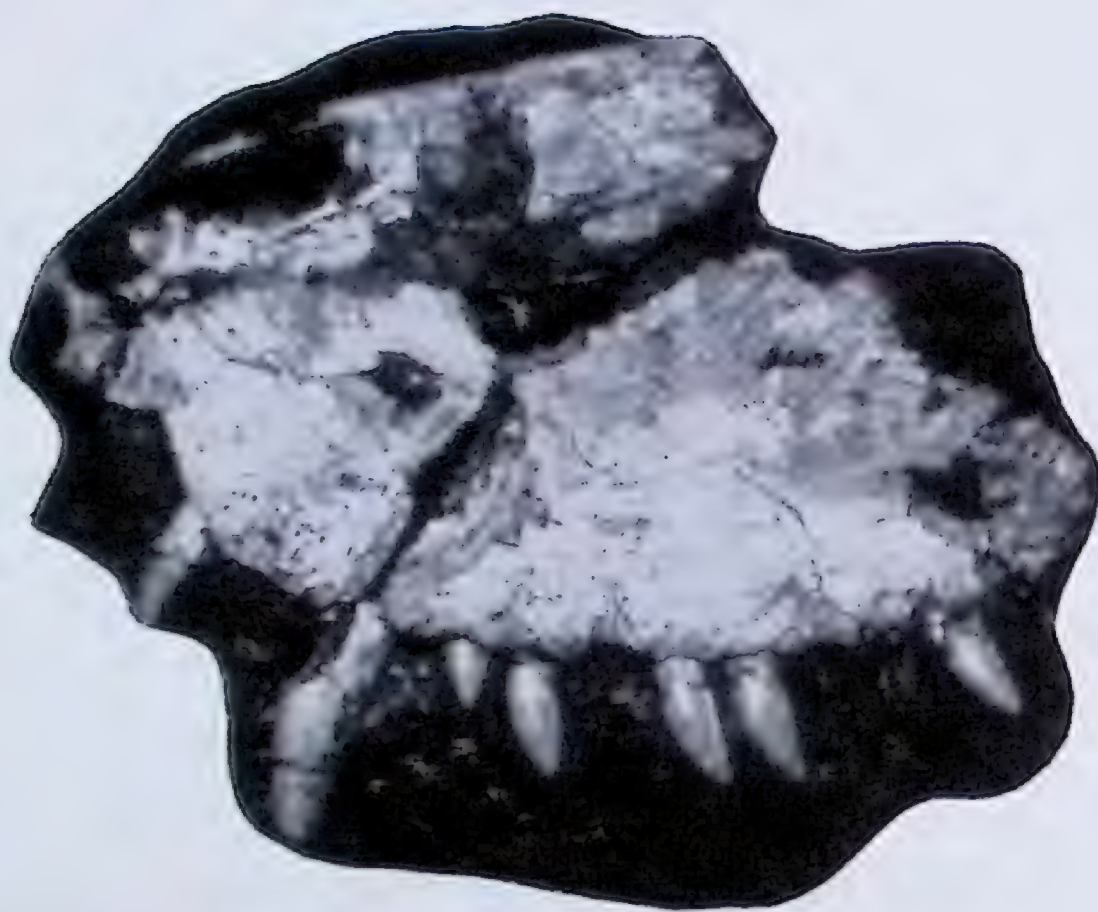
Bathynathus borealis Leidy

(Figure 5; Plate II)

The type of this species (Acad. Nat. Sci. of Philadelphia, 9524) consists of the left side of the face from just in front of the orbit to the external naris. It is by far the largest vertebrate specimen so far collected from the Prince Edward Island red beds and represents the largest animal yet recognized in these deposits. The maxilla containing a number of teeth is nearly complete, the septomaxilla is preserved, and some of the nasal is intact. A little of the premaxilla is also preserved. The position and general form of the naris can be determined from the matrix. The preservation of the specimen shows without question that the facial part had become separated from the rest of the skull before burial, but there is evidence that the premaxilla and one maxillary tooth were lost after discovery. The circumstances leading to the specimen's acquisition by the Academy of Natural Sciences are related by Leidy (1854, p. 327):

"In the last visit of the enthusiastic and distinguished geologist, Sir Charles Lyell, to this country [United States], he informed me that Mr. J. W. Dawson, of Pictou, Nova Scotia, had received from Mr. D. McLeod, for disposal, a fragment of a jaw of a large saurian animal, which was found in the New Red Sandstone of Prince Edward's Island. Mr. Lyell sent me an outline drawing of the jaws: and with the disinterestedness of a cosmopolite philosopher, recommended Mr. Dawson to send the specimen to the Academy of Natural Sciences of Philadelphia, in preference to disposing of it abroad. It was accordingly sent to the latter [sic!] place and was purchased by Messrs. Isaac Lea, William S. Vaux, and myself, and was presented to the Academy . . ."

PLATE II



Bathygnathus borealis Leidy, holotype, Phil. Acad. Nat. Sci. no. 9524. Approx. X.4 nat. size.

Leidy was uncertain about the creature's affinities but inquired (1854, p. 329), "Was this animal probably not one of the bipeds, which made the so-called bird tracks of the New Red Sandstone of the valley of the Connecticut?"¹ Owen (1876) recognized the specimen as an upper jaw and noted resemblance between *Bathygnathus* and the African theriodonts. But he misinterpreted many features of the specimen. Von Huene (1905) and Case (1905) independently recognized the sphenacodont nature of the specimen and confirmed that it is an upper, not a lower jaw as assumed by Leidy.

I have examined the specimen and intend the following remarks to supplement earlier descriptions. The rostral part of the skull was very deep, with a maximum vertical diameter (above the fifth tooth) of 130 mm. The dental margin of the maxilla is strongly curved with a wide and deep sphenacodont notch anteriorly. Seven functional teeth, an impression of an eighth, and the erupting tip of a ninth are preserved, but there are at least four vacant alveoli. The preservation posteriorly is not sufficiently good to be sure, but I believe that no more than 13 maxillary teeth were present, a smaller number than usually occurs in any *Dimetrodon* except *D. grandis*. Nine postcanine teeth occupy a distance of 115 mm.

The third maxillary tooth is a relatively huge, long and slender canine, the second of the usual pair (the alveolus in front is 15 mm long, and only a little smaller than that containing the tooth). The first maxillary tooth appears long and slender, but this is because it has been partly expelled from its socket. The fourth tooth is in process of eruption, but its alveolus is only 10.5 mm long. The structure of the teeth seems identical to that of many *Dimetrodon* teeth compared, but the large canine has a less quadrangular basal section than many *Dimetrodon* teeth of similar or smaller size. Vertical fluting of the lingual surfaces of the crowns, though discernible, is less pronounced than on some *Dimetrodon* teeth.

The maxilla is broad, deep, and flat-sided with a large pre-orbital hollow. It is sculptured in characteristic *Dimetrodon* fashion by long narrow sulci, fine reticular grooves, and small foramina. A pit above the first and second tooth is apparently an artifact and may be a puncture inflicted by another animal. The bone is nearly complete along most of its posterior edge which joined the jugal, but the lacrimal edge is lost. The nasal bone, in so far as interpretable from the part remaining and the cast of its inner surface *in matrix*, was of characteristic *Dimetrodon* form. Dorsolaterally, it formed a broad rugose longitudinal ridge, below which the side of the face is broadly excavated. A septomaxilla, clearly shown in Leidy's plate, is also of characteristic *Dimetrodon* form, but its surficial exposure between the nasal and maxilla is a little broader than in various *Dimetrodon* skulls compared.

The specimen is equal in size to the large sphenacodont, *Sphenacodon ferocior* of New Mexico, and is surpassed among dimetrodons only by the relatively late *D. grandis* and some *D. gigashomogenes*. Thus Romer and Price (1940) suggested that *Bathygnathus* seems a more advanced sphenacodont than would be expected in rocks of Stephanian age (as those on Prince Edward Island were then thought to be). That the animal is indeed advanced is shown also by the reduced number of maxillary teeth which is apparently within the range of *D. grandis* (13-16 usually).

¹ It has often been stated that Leidy attributed *Bathygnathus* to the dinosaurs, and in retrospect this is implied by his words. In fact, Leidy nowhere mentions "dinosaur," which was a concept still little understood, but calls the animal a "carnivorous lacertilian." He notes that the teeth resemble *Megalosaurus* and was thus certainly among the first to suspect the true nature of the New England "bird" tracks, although even four years later this was not yet apparent to Hitchcock, who still attributed the Connecticut Triassic trackways to avian origin (*Ichthyology of New England*).

Individual teeth seem relatively larger than in most dimetrodons and *Sphenacodon*. If, as I suspect, the lacrimal is abbreviated with respect to the length of the rostrum, this also indicates an advanced grade. This character and the existence of a large precanine tooth may distinguish *Bathygnathus* from *Sphenacodon ferocior*. The close coincidence of form between *B. borealis* and *Dimetrodon limbatus* is graphically shown in Figure 5. It will be noted there that the part of the *Bathygnathus* face preserved is relatively longer than in the *Dimetrodon* and the teeth are relatively larger.

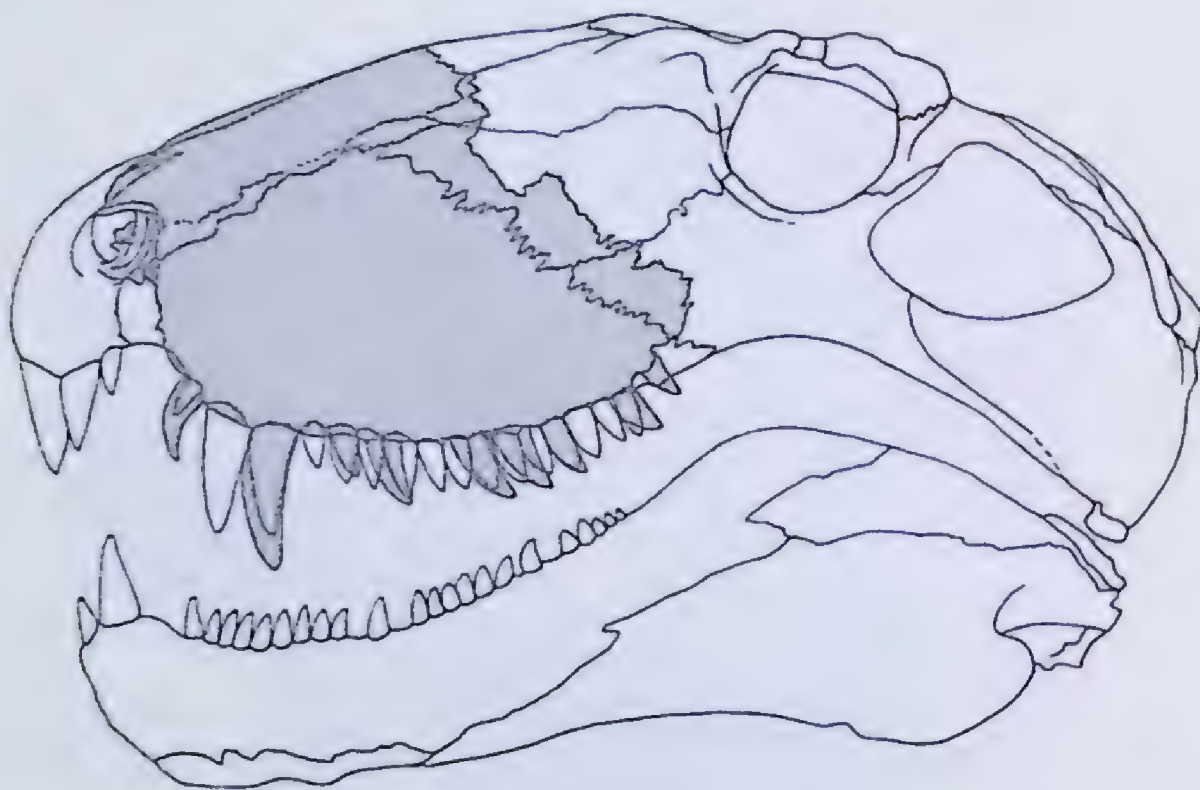


FIGURE 5. *Bathygnathus borealis* Leidy compared with *Dimetrodon limbatus*. *Bathygnathus* specimen shaded, *Dimetrodon* after Romer & Price. Drawings reduced to same scale, *Bathygnathus* approx. X.25 nat. size.

Bathygnathus is easily distinguished from the large Guadelupean *Steppesaurus* Olson and Beerbower, in which the teeth are more elongate, relatively far apart, and more heavily fluted than in *Bathygnathus*. Relationship with the small French Autunian sphenacodontine *Neosaurus cynodus* (Gervais) must be distant, because that species has four precanines, and none of the teeth have serrated edges. Resemblances to the English Autunian sphenacodontine *Oxyodon britannicus* von Huene are perhaps as close as to *Sphenacodon*, to which *Oxyodon* may be closely allied (the type of *O. britannicus* was, like *Bathygnathus*, early mistaken for a dinosaur, and it was again von Huene who first recognized its true affinities).

A small fragment of a mandible from near Keppoch contains a tiny piece of matrix on which are seen the impressions of several characteristic sphenacodont dental serrations. The specimen was much smaller than *Bathygnathus borealis*, and there is no reason to suppose that it pertained to that species.

Bathygnathus borealis is potentially of great taxonomic interest. It was the first pelycosaur ever discovered and the name first appeared in print in the Proceedings of the Academy of Natural Sciences of

Philadelphia of October 18, 1853 (Leidy, 1854a, 6: 404). The accompanying description is inadequate, but a full account illustrated by a beautiful coloured plate appeared almost simultaneously in the Journal of the Society (Leidy, 1854b). This paper was abstracted at length in the American Journal of Science (Leidy, 1855) and has been widely quoted on several subsequent occasions. The name *Bathygnathus* thus would have priority over *Dimetrodon* or *Sphenacodon*, one of which it may some day prove to be. Romer and Price (1940) suggested that on geographic grounds *Dimetrodon* was the more likely candidate for suppression. Now, on morphological grounds this appears even more probable. Since, however, nothing resembling a *Dimetrodon* neural spine has been found on Prince Edward Island and since some cranial differences from *D. limbatus* have been noted, I prefer to continue to distinguish the animals taxonomically at the generic level.

Genus cf. *Mycterosaurus* Williston
(Figure 6)

A small dentary bone from a boulder of hard calcareous clay breccia at the Spring Valley locality (P-6108) represents a small reptile which with reservation may be compared to *Mycterosaurus*. The specimen, NMC 10000, is only visible in lateral aspect, and about a third of its outer wall has been lost to weathering. Otherwise, preservation is complete, and most of the teeth are retained. The bone has a complete length of 45.4 mm, of which the tooth row occupies 34.0 mm. The maximum height of the dentary is 6.2 mm, and the longest teeth are about 2.7 mm high.

The side of the dentary is composed of very thin, delicate bone. Its outer surface is only lightly sculptured, and no specific pattern can be discerned. There are a few foramina beneath the bases of some of the anterior teeth. The bone is flattened from side to side. The lateral outline is broadly undulating with some downward bending anteriorly, a little upward bowing of the ventral edge in the middle third of its length, and slight vertical expansion beneath the posterior part of the tooth row. Posteriorly, the bone tapers to a point, the dorsal edge rising gradually, the ventral edge more rapidly. Much of this posterior part was in contact with the angular, but the exact area of overlap cannot be determined.



FIGURE 6. Genus cf. *Mycterosaurus* Williston. Left dentary, NMC 10000, from Spring Valley (Loc. P-6108). Approx. X1.3 nat. size.

There were 29 closely-spaced teeth, of which all but the first and seventeenth are preserved. These are arranged in a single row along the dorsal edge of the dentary and supported at the labial side by a low wall of bone. The bases of the teeth are attached to the bone by spongy tissue much as in *Captorhinus*. Matrix has been removed from the space formerly occupied by the seventeenth tooth revealing a small cavity at the base of the eighteenth tooth. A similar pit occurs in the root of the twenty-first tooth. Both cavities are more anterolaterally situated than would be expected if they had been sites for developing replacement teeth, but they probably resulted from resorption related to tooth replacement. The only

other evidence of replacement activity in the jaw is the relatively small size and crowded condition of the twenty-fifth tooth (the lingual sides of the teeth are not visible).

Long cylindrical, enamel-free roots contain large pulp spaces, but the short crowns—seen in two broken teeth—are solid. Crowns of the anterior teeth are sharply pointed, a little recurved, and hooked lingually. They bear minute carinae, and the lingual surfaces are marked by indistinct vertical fluting. Farther back the teeth become heavier with straight blunt (in lateral aspect) crowns, some of which have a slightly greater circumference than their roots. Viewed in the longitudinal plane, the roots of the teeth near the middle of the series are seen to expand mesially toward the base which must be quadrangular in section and wider than long. This accentuates the inwardly hooked appearance of the crowns.

The first tooth, to judge from the position of its alveolus, projected strongly forward, the second is similarly, but less sharply inclined, and the third attains a nearly vertical position.

The systematic position of this little jaw is not easy to determine in spite of its excellent preservation. Conical, isodont, acrodont teeth are characteristic of amphibians and many early reptiles, and mandibular dentitions are not often adequately described in these. The position of the teeth atop a high dentary bone that lacks a strong labial edge suggests that the animal was not an amphibian; absence of labyrinthine structure at least shows that it was no labyrinthodont.

The light sculpturing of the side of the dentary distinguishes the bone from many cotylosaurs, although implantation of the teeth resembles *Captorhinus*. Cotylosaurs in general have fewer teeth than this animal, but some, for example the Russian Permian *Nycteroleter* and *Nyctiphruretus*, have between 25 and 30 teeth in each dentary. The dentary resembles that of *Nycteroleter* in its elongate slender form, and the slight downturning of the ventral edge anteriorly. The mandibular dentition of *Nycteroleter eneptus* Efremov is very imperfectly known, despite Efremov's attractive reconstruction (Efremov, 1940; fig. 21). Teeth of other species of *Nycteroleter* described by Chudinov (1957) resemble the present specimen in lateral aspect but are very unlike them when seen from behind, the teeth of the Russian animal having almost straight lingual sides. Photographs show a higher degree of sculpture on the dentary of *Nycteroleter*. The present dentary is not so deep or relatively short as in *Nyctiphruretus acudens* Efremov, but the teeth are similar in many respects (Efremov, 1940; Pl. 29, fig. 3). The teeth of *Nyctiphruretus* are, however, less crowded and more "haarnadelartig," and the bases of the roots, although quadrangular in cross-section, are not enlarged there as in the present specimen.

The dental characters of this specimen may be approached most closely in mandibles of certain edaphosaurs and *Eothyris* where a high degree of isodonty prevails. But the Edaphosauridae and known Caseidae can be eliminated from further consideration by their very different jaw proportions and numbers and specialization of the teeth; *Eothyris* has a very differently-shaped dentary (to judge from undescribed material from New Mexico). No positive statement is possible regarding *Mycterosaurus* whose mandibular teeth are inadequately known. There are, however, distinct resemblances to the related *Nitosaurus jacksonorum* Romer from the early Permian Cutler formation of New Mexico. The jaw figured by Romer and Price (1940, fig. 70) is a little larger than the present specimen, and the teeth appear somewhat more conical and lack long cylindrical roots. But

they are relatively long and slender for a pelycosaur and are closely-spaced and pointed. As the last few teeth are missing from the specimen, it is unknown if these became more obtuse. The tendency for the anterior end of the dentary to arch downward and the consequent projection of the first few teeth is even stronger in *Nitosaurus* than in the specimen from Prince Edward Island.

Associated in the same boulder with the dentary was a single tooth of reptilian character, NMC 10017, which, although very similar to those near the middle of the dentary series just described, is at least twice as large as any of them. Its base is notched fore and aft in the same way, suggesting that it had been shed or was nearly ready for replacement. There is every reason to believe that this tooth and the jaw pertain to the same species, but the large tooth may be from the upper jaw, which in both *Nitosaurus* and *Mycterosaurus* contained larger teeth than the mandible. It has a form that could be expected in primitive edaphosaurs. If this is true, the affinities probably lie with the nitosaurids, and the resemblance may have been closer to *Mycterosaurus* than to *Nitosaurus*, whose upper teeth are more acutely pointed than this tooth. The dentary of *Mycterosaurus* does not appear to turn downward in the symphyseal area, and the present jaw is thus intermediate between it and *Nitosaurus*. On the other hand the posterior ascending process of the dentary in the Prince Edward Island animal appears almost identical to that figured by Romer and Price (Plate 21) in *Mycterosaurus*.

Association with the peculiar metatarsal next to be described raises the question: might not this dentary belong to *Trichasaurus*? The dentary seems small in relation to the toe bone, but nothing is known about the jaws and teeth of *Trichasaurus*. If the nitosaurids and caseids are related, the likelihood that the dentary and metatarsal both belong to *Trichasaurus* is good, for this genus probably belongs to one or the other group; nitosaurid metatarsals are unknown.

Trichasaurus Williston

(Figure 7)

From the stratigraphic viewpoint perhaps the most interesting vertebrate fossil yet collected on Prince Edward Island is the first right metatarsal and articulated proximal phalanx of a caseid pelycosaur, NMC 9991. The specimen was found in one of the clay-breccia boulders at the Spring Valley locality (P-6108).

The metatarsal has a greatest transverse diameter of the proximal end of 14.3 mm and of the distal end of 12.0 mm, and the least diameter of the shaft is 8.7 mm. The greatest axial length is 15.7 mm. Its shape is very distinctive; opposite ends are slightly twisted so that they lie in intersecting planes. The bone is dorsoventrally flattened throughout. The proximal end, when viewed from above, has roughly the outline of a 30 degree to 60 degree triangle whose shorter, medial leg formed a thickened "heel" at the inner side of the digit. The longer leg of the triangle is broadly and irregularly saddle-shaped where it articulated with the corresponding distal tarsal. The proximal apex of the triangle is blunt, and the bone is thickened. Near the middle, the saddle-shaped tarsal facet curves gradually upward and becomes confluent dorsally with a well-defined pit in the upper side of the metatarsal. This pit accommodated the distal edge of the tarsal when the digit was strongly flexed at the tarso-metatarsal joint and provided a considerable arc of vertical movement. There is no trace of a pressure facet

opposing the second metatarsal. The planter surface of the proximal end shows the same triangular outline, uncomplicated by a pit but containing a poorly-defined peroneal tuberosity beneath the apex.

The articular surface at the distal end is considerably shorter than the maximum width of the bone at this end. It consists of two confluent flattened condyles, of which the lateral one is considerably the larger. The articular surface faces diagonally downward so that it is not visible in dorsal aspect.

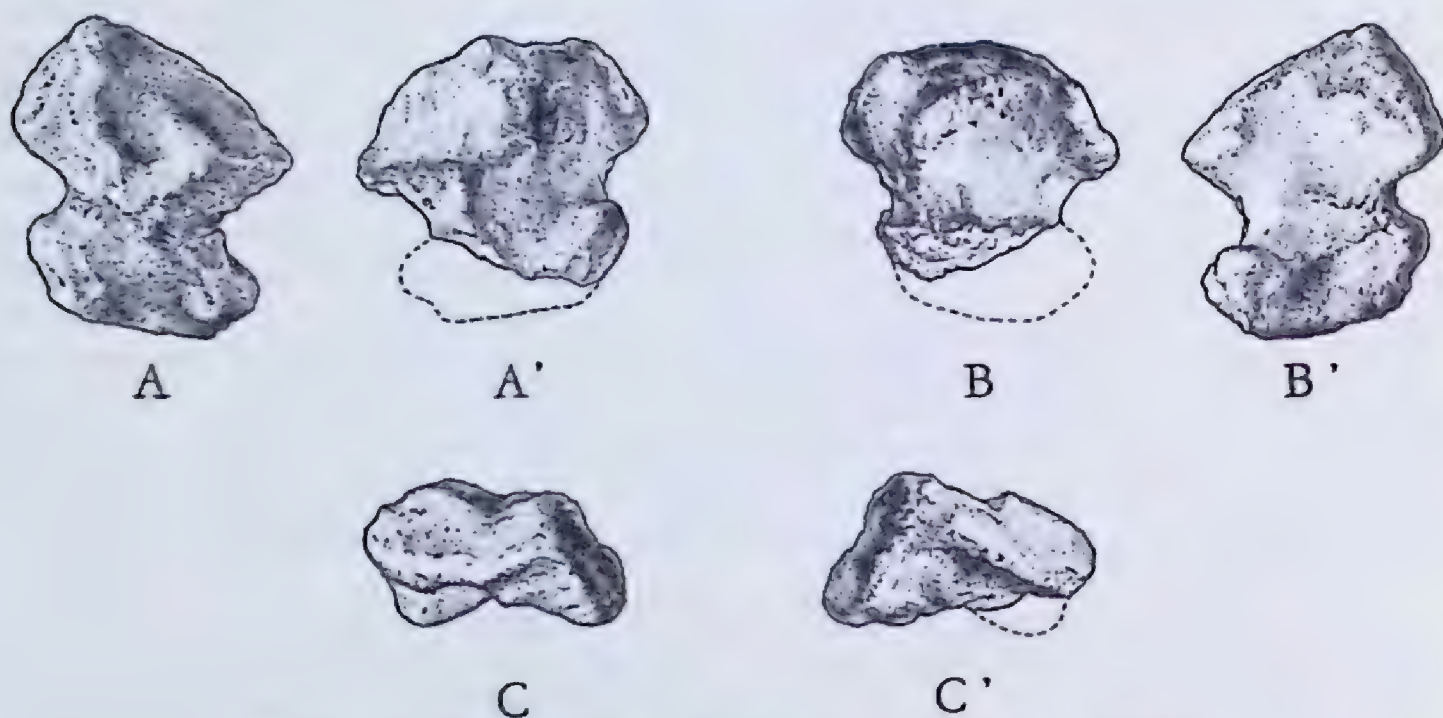


FIGURE 7. *Trichasaurus* sp. Right metatarsal I. NMC 9991, from Spring Valley (Loc. P-6108). (A) from above, (B) from below, (C) proximal aspect. Approx. X1.5 nat. size. For comparison, the opposite metatarsal of the type of *T. texensis* Williston (Chicago Nat. Hist. Mus. - U.C. 652) is drawn to the same scale, approx. X1.5 nat. size. The apparent absence of a sharp proximal apex on this bone in A' and B' is owing to its slightly different position. It is clearly seen in C'.

The phalanx, of which only the proximal half remains, was found in natural articulation with the metatarsal. Its proximal articular surface is the counterpart of that on the metatarsal and is therefore broadly visible from above. This bone has a greatest transverse diameter proximally of 12.0 mm, but it narrows rapidly distally to a shaft diameter of only 5.4 mm.

The form of the metatarsal is unique, but a somewhat similar bone is found in *Casea broilii* Williston and *Trichasaurus texensis* Williston. An incomplete first metatarsal preserved with the type skeleton of *T. texensis* (Chicago Nat. Hist. Mus. - U.C. 652) is very similar to the present specimen. All features of one occur in the other, but the relative position of the proximal apex differs. In *Trichasaurus* it lies more dorsally, in the Prince Edward Island specimen more horizontally, resembling *Casea broilii* more in this respect. The thickness at the proximal end is thus relatively greater in *Trichasaurus*, and the apex appears more obtuse in dorsal aspect. In both *Trichasaurus* and *C. broilii* the "heel" is also relatively shorter and evidently differently oriented in *Casea*. Considering the bone as a whole, however, none of these differences seem very significant in view of the resemblances.

Trichasaurus may be related to *Casea*. Its ancestors are unknown and stratigraphically it occurs a little lower in the Permian sequence than *C. broilii*. Its first metatarsal is perhaps more like that of *C. broilii* than any other pelycosaur except the present one, but according to Olson (pers. comm.) whereas some caseids tend to develop metatarsals of this kind, not all do, and "Even *Edaphosaurus* tends in this direction." There is no suggestion of *Edaphosaurus* on Prince Edward Island, and I believe the present specimen can best be assigned to *Trichasaurus*.

THE AGE OF THE RED BEDS

The question of the age of the red beds on Prince Edward Island has confounded geologists for over a century. The problem results from the separation of the rocks from the mainland, deceiving structural conditions, the nature of red bed lithology and its sedimentary structures, and most importantly, the puzzling and seemingly contradictory implications of the few known fossils. The earliest ideas about the age of the red beds were derived mainly from lithological and palaeobotanical evidence.

Early dating. Sir William Dawson's second contribution to the geological sciences is evidently the first attempt to date the rocks of Prince Edward Island (Dawson, 1842). He emphasized lithological similarities between the beds southeast of Charlottetown and the "Coal Formation" of Nova Scotia. An analysis of fossil wood from near Gallows Point seemed to support this, and there has since been little question that whatever the age of the grey and brown beds along the south shore, they are older than the red rocks exposed elsewhere. Gesner (1846) observed lithological differences between the dark-coloured rocks of Governor Island and the red beds of Prince Edward Island, pointing out the resemblance of contained plant fossils to those of the coalfields of the opposite coast. The rocks at Gallows Point are said to be of the "Coal Formation." Later, Dawson (1848) concluded that the age of the rocks was uncertain but definitely post-Carboniferous and quite possibly equivalent to the Triassic red sandstone of the Connecticut Valley. But he acknowledged his inability to distinguish plants in the lower beds from some found in the "newer coal formation." Dawson's periodic examinations of the problem from this date onward are characterized by progressive restriction of the presumed Triassic part of the section and continuing uncertainty about the age of older deposits.

For many years after discovery of *Bathygnathus*, the animal was used to support the supposed presence of Triassic rocks. At first, however, Leidy seems to have had no clear idea of the age of the animal, which was inferred from a letter by Dawson stating that the red sandstones that contained the fossil "will be equivalent to the New Red of western Nova Scotia and Connecticut, and probably Triassic or Permian" (Leidy, 1854, p. 330). A footnote to Dawson's letter quotes Lea as believing "there are many reasons in favour of referring them to the superior strata of the Permian series," and in *Acadian Geology* of 1855, Dawson notes supposed resemblances between *Bathygnathus*, and *Thecodontosaurus* and *Palaeosaurus*, which he mistakenly took for Permian (=lower new red) genera. Dawson's study of fossil wood from various south shore localities (1854) furnished "an argument in favour of the Permian date" of the "new red sandstones." He soon returned to his earlier ideas, for in a well-documented study (Dawson & Harrington, 1871) the brown, grey, and red sandstone and shale around Orwell, Pownal, and Hillsborough bays, Governor Island, and on the coast between North and West capes were assigned to the "Newer Carboniferous Age." The bright red, often calcareous sandstones, soft red shales with

concretionary limestones, and conglomerates were called "Trias," and two members were recognized as possibly equivalent to the Bunter and Keuper of Europe. Some fossil plants were believed to be of Triassic age, but it is obvious that the authors were influenced by *Bathygnathus* and their interpretation of the sequence of the layered rocks. This work evoked a pedantic reply by H. G. Geinitz (1872), who could find no evidence in the fossil flora for any but a lower Diassic (=Lower Rotliegende) age.

Richard Owen (1876) stated that the presence of *Bathygnathus* was in no way "indicative of a Liassic age, and the majority of instances weighs in favour of a Permian Period." But Dawson continued to cite *Bathygnathus* and some very uncertain plant remains as evidence of Triassic age. In 1874 he designated the beds previously assigned to the coal formations or Carboniferous as "Permo-Carboniferous," and four years later concluded that these Permo-Carboniferous rocks were a continuation of "beds which overlie the Coalfield of Pictou and extend into Prince Edward Island" (Dawson, 1878b, p. 38).

In 1881 Francis Bain described a collection of fossil plants from the Hillsborough Bay district, and there then seemed no doubt that some rocks on the Island belonged to the Permian system. Bain and Dawson (1885) then attempted to accommodate the fossils to the apparent lithological divisions within the rock sequence by proposing a tripartite arrangement in which the upper beds were Triassic, the lower were Permo-Carboniferous, and all between were lower Triassic, or more probably Permian. They recognized that the area occupied by the older strata was considerably larger than Dawson and Harrington supposed, and the same year Ells (1885) suggested that all sandstones and shales were Permo-Carboniferous, and that Triassic deposits, if present, were of very limited extent. Dawson was still uncertain about the Permian, however, and in the 1891 edition of *Acadian Geology* he suggested that certain *Dadoxylon* wood implied an age older than the New Red Sandstone. He there reiterated the conviction that rocks exposed along the south coast "if not Permian, may represent the upper beds of the Newer Coal Formation." He had no doubts, however, about the presence of Triassic sediments above.

I. C. Russell (1892) rejected Dawson & Harrington's Triassic assignments, holding that the fossils used were inconclusive at best. Current palaeobotanical opinion would support Russell (F. Hueber, pers. comm.). Russell concluded that none of the red beds were related to the Newark series, and on the palaeobotanical authority of F. H. Knowlton assumed that the lower beds at least were Permo-Carboniferous.

Two vertebrate palaeontologists, E. C. Case (1905) and F. von Huene (1905), independently and almost simultaneously recognized the true nature of *Bathygnathus* and eliminated the principal basis for attributing the New London red beds to the Triassic system. Both authors referred the rocks to the Permian.

Holden (1913) studied additional fossil plants from south shore localities and stated that the presence of *Tylodendron* left no doubt that the rocks were of Permian age. In addition to *Tylodendron*, she listed *Sternbergia* pith casts and *Cordaite*s leaves and wood. The most recent consideration of a florule from Prince Edward Island was by Darrah (1936, 1937).¹ The specimens were collected by Bain in 1875, at Miminegash and included *Walchia dawsoni*, *Callipteridium* aff. *pteridium*, *Pecopteris arborescens*, *Alethopteris grandini*, and *Sphenophyllum oblon-*

¹ This paper, though published in 1937, was read at Herleen in 1935. Identifications of the plants differ somewhat from the revised list given in 1936.

gifolium. The assemblage was believed to resemble the "typical" Monongahela (=Stephanian) flora of Pennsylvania. Darrah's work revived questions about the age of *Bathynagathus*, for "in the Southwest sphenacodont species of equal size are known as yet only in association with an Autunian flora" (Romer & Price, 1940, p. 322).

Recent progress. Some important new data have recently come to light. The ostracod *Carbonita inflata* (Jones & Kirkby) from surface rocks at Little Miminegash Pond is a Carboniferous species which occurs in Pictou rocks of the Maritimes (Copeland, 1957).

A variety of Pennsylvanian spores has been recovered in well cuttings from the western part of the Island. Prest (1961) reports Stephanian types at a depth of 1,730 feet in a hole drilled about ten miles west of Summerside. According to P. A. Hacquebard and M. S. Barss (pers. comm.), the same hole yielded a Westphalian "D" (Pictou) assemblage between 2,550 and 3,970 feet. They report Stephanian spores between 1,720 and 1,740 feet in a hole drilled about eleven miles to the north, near Port Hill, and from about 10 to 2,900 feet at another site near MacDougall, about seven miles northeast. Both holes also penetrated Westphalian "D" and "C" beds commencing at 2,850 and 3,070 feet, respectively. Westphalian "D" spores occur at a depth of 600 feet in a hole drilled at Miminegash, and Prest (1961) states that plant microfossils from surface rocks on Governor Island indicate a Middle or Upper Pictou (=Westphalian) age.

Thus previous work gives no reason to attribute any of the red beds on Prince Edward Island to the Triassic system. There is now enough palaeobotanical evidence to show that late Pennsylvanian sediments occur at or very near the surface at Miminegash and Governor Island, and perhaps also at Gallows Point. The question of where to place the rest of the red bed section remains. Vertebrate fossils contribute to the solution of this problem.

The evidence of fossil vertebrates. Useful vertebrate fossils have been found in three general areas: between New London and Malpeque Bay in the north-central part of the Island; on the coast of Hillsborough Bay on the south shore, and at Seacow Head to the west. The vertebrates from the north-central area are the most illuminating.

So similar is *Bathynagathus* to *Dimetrodon* that had it been found in the Texas red beds, it would surely have been assigned to that genus, perhaps even to *D. limbatus* (Cope), the common *Dimetrodon* of the Admiral and Belle Plains (upper Wichita) beds in Texas. On geographic grounds there is certainly more reason to associate *B. borealis* with the vertebrate assemblage from the Spring Valley and nearby localities than with the Stephanian florule at Miminegash or the spores on Governor Island.

Other vertebrates from the north-central area are most closely allied to animals from upper Wichita and lower Clear Fork deposits of Texas, as indicated below:

P.E.I. Locality	P.E.I. Species	Closest Related Texas Species	Stratigraphic Range of Texas Species
P-6108	<i>Trichasaurus</i> sp.	<i>T. texensis</i>	Arroyo fm.
P-6108	Genus cf. <i>Mycterosaurus</i> sp.	<i>M. longiceps</i>	Clyde fm.
P-6111	<i>Seymouria</i> sp.	<i>S. baylorensis</i>	Belle Plains fm.— Arroyo fm.
P-6108	Genus near <i>Eobrachyops</i>	<i>E. townendae</i>	"Clear Fork"

Of the Texas species, only *Seymouria baylorensis* is known from rocks beneath the Wichita—Clear Fork boundary. Ancestors of none of them

are known with certainty in Pennsylvanian rocks (but their phylogenies are very imperfectly known). *Mycterosaurus* and *Seymouria* are probably relicts of earlier Permian and Pennsylvanian times. I believe *Trichasaurus* is related to *Casea*. The closest known *Casea* ancestor is probably *Eothyris* of the Texas Belle Plains and New Mexico Cutler formation. Because wide morphological differences separate *Eothyris* from the very specialized caseids, evolutionary change must have been very rapid during early caseid development, just as Olson (1954) shows it to have been in the latter part. The metatarsal bone of *Trichasaurus* sp. from the Spring Valley locality is so similar to the bone in *T. texensis* that a close relationship has been assumed. The only other pelycosaur with which it might be associated is *Casea broilii*, and if in fact it is a *Casea*, this would not seriously affect the time-stratigraphic assignment. *C. broilii* occurs in Texas in the overlying basal Vale formation, and the genus is unknown below this level. In view of the rapid caseid evolution at the time, homotaxis is probably not an important consideration, and the Spring Valley animal suggests an early Leonardian Age (=early Artinskian, approximately). The associated fossils support this conclusion.

Vertebrates from the Hillsborough Bay region are less instructive. *Eryops* evolution was relatively conservative in the late Palaeozoic. There is presently no satisfactory means of distinguishing the several species that have been described, and Permian "species" are placed in *E. megacephalus* by most contemporary students. The premaxilla from Lobster Point (P-6109) cannot be distinguished from *E. megacephalus* of the Texas Permian. Its relatively small size (still well within the observed range of *E. megacephalus*) could reflect immaturity and may have no bearing on the animal's evolutionary grade. *Eryops* was almost certainly in existence before the end of the Pennsylvanian period and evidently disappeared before the end of Leonardian time.

The xenacanth shark tooth from Gallows Point is important in setting an upper limit for the age of the chocolate-brown sandstones not later than early Leonardian, when *X. texensis* disappears from the Texas section (at the top of the Wichita group). The resemblance to the late Pennsylvanian *X. compressus* is as close as to *X. texensis*—a satisfactory basis for separating single teeth of these species is still to be found. It is therefore possible that this tooth is from a Stephanian or older animal (the broad genus *Xenacanthus* can be recognized as far back as the Devonian).

The relationship of the ophiacodont from Squaw Point (P-6004) is too uncertain to permit useful conclusions about its age. The same is true of the tiny diadectamorph jaw fragment from Selkirk Park (P-6008).

The diadectid zygapophysis from Selkirk Park (P-6009) could represent either *Diadectes* or presumably *Desmatodon*, whose range evidently extends downward into the Stephanian (Conemaugh). On size grounds alone, reference to the Permian *Diadectes* seems more probable since this vertebra was at least as large as some from the upper Admiral formation in Texas. European diadectids are from middle Rotliegende deposits (Olson, 1947).

The presumed dipnoan burrow at Gallows Point has no stratigraphic importance in the present connection. In Texas such structures occur in the Clear Fork beds.

I believe the evidence most probably implies an early Permian age for the fossiliferous strata throughout the Hillsborough Bay district. However, in view of the proximity of Westphalian deposits on Governor Island and the inconclusive palaeobotanical evidence from Gallows Point, it seems prudent for the time being to call these beds Permo-Carboniferous. Whatever their age they are older than the red beds to the north.

What has been said of the xenacanth tooth from Gallows Point is also applicable to the specimen from Seacow Head (P-6112), where, however, there are no fossils that can be used to place a lower limit on the age of the rocks. They are older than those of the north-central area and possibly contemporaneous with the chocolate-brown sandstones at Gallows Point.

Nothing in this analysis conflicts with current palaeobotanical conclusions. Though the age of much of the red bed sequence on Prince Edward Island remains unknown, it is now clear that—

- (1) The age of the rocks differs from place to place;
- (2) The oldest known strata occur in the southern and western parts of the Island;
- (3) Younger beds appear in the north-central part;
- (4) There is no evidence of the presence of Triassic rocks;
- (5) The oldest known sediments are of late Pennsylvanian age;
- (6) Beds of early Permian (Leonardian) age are present.

These conclusions, though more firmly based, are not greatly different from the ideas of Dawson, Russell, and others, expressed three-quarters of a century ago.

SOME IMPLICATIONS AND INFERENCES

The vertebrates described in this paper are closely related to members of the early Permian red bed faunas of the southwestern United States. The composite assemblage contains no certain tetrapod genus with known European species, and the xenacanth shark seems at least as similar to North American species as to any from the European Permo-Carboniferous.

Elsewhere in North America, roughly contemporaneous "red bed" assemblages from the Dunkard beds of southeastern Pennsylvania and adjacent states are geographically closest to Prince Edward Island. The composite assemblage from the Washington and Greene formations (Romer, 1952) differs markedly from that of Prince Edward Island in its more diversified fish and amphibian components. Only the ubiquitous xenacanths and *Eryops* are shared. Possibly, though by no means probably, the diadectid *Desmatodon* occurs in both, but the pelycosaurian elements are very different. The great predatory sphenacodonts, so common in Texas, New Mexico, and Oklahoma, and represented on Prince Edward Island by *Bathynathus*, are unreported in the Dunkard. *Edaphosaurus*, which is the principal pelycosaur of the Dunkard, is only common locally in Texas, very rare in New Mexico, and unknown on Prince Edward Island. This faunistic peculiarity probably reflects an important difference in depositional environments—*Edaphosaurus* was a creature of the swamps. The Washington and Greene formations were no doubt deposited under moister conditions than the red beds of Prince Edward Island.

Another fauna of interest is the Pennsylvanian (probably late Westphalian) red bed assemblage from Danville, Illinois, which in earlier days was assigned to the Permian. It is comprised mainly of fish, among which only *Xenacanthus compressus* may occur on Prince Edward Island. There are some amphibians here without relatives on Prince Edward Island, and a few reptiles. The ophiacodont from Squaw Point suggests, at most, only family resemblance between the reptiles of the two assemblages.

The Danville and Dunkard faunas were probably successive in time and are not widely separated spatially. Danville, however, which is the oldest known Permo-Carboniferous red bed assemblage, may reflect a less swampy environment than the other (*Edaphosaurus*, for example, which

occurs in Pennsylvanian deposits elsewhere, is unreported at Danville). The Prince Edward Island fauna that was at least partly contemporaneous with the Dunkard faunas represented even drier conditions.

If, as I suppose, sediments exposed around Hillsborough Bay are approximately as old as the lower Wichita beds of Texas, their more regular sedimentation and more uniform red coloration suggest the existence of more uniform red bed sedimentary conditions here at an earlier time than in Texas. That the environment became drier and more sharply seasonal earlier on Prince Edward Island is suggested by the dipnoan burrow in this part of the section. Although dipnoan remains are not uncommon in Wichita beds, there is no evidence of aestivation beneath the basal Clear Fork. There is here a parallel to the development of the progressive regional drying witnessed by the Cisco-Wichita-Clear Fork sequence, with the Permian Dunkard assemblages providing a glimpse of the life and habitats in moister environments, such as is offered by the famous Geraldine bone bed in the Wichita sequence in Texas.

The red beds of Prince Edward Island comprise mainly sandstones, claystones, clay breccias, and conglomerates. They have been described repeatedly, for example by Dawson (1855), Dawson & Harrington (1871), and Milligan (1949). In order now are a few comments on the probable significance of a few geological observations resulting from my palaeontological work in the central third of the Island. Conditions may differ in other places, but perhaps not enough to negate the following generalizations.

The sandstones are mainly primary detrital arkoses. The mineralogical composition described by Milligan—quartz together with both fresh and altered feldspars, biotite, etc., mixed with red clay—suggests that deposition occurred not far from a source region with youthful drainage. The coarser clastics are generally cross-bedded, but in some cases topset lamination in fairly uniform fine sands is very regular over extended areas. Some foreset lamination is so broad that it might even be confused with true bedding and thus might cause erroneous estimates of the thickness of the section.

The red colour of the rocks is so general and uniform throughout most of the section that the absence of variegation is very apparent. Except for limited freshwater limestones at Miminegash and Gallows Point, the only grey or green coloration I have seen is obviously a result of reduction of ferric oxide along joints and at shale-sandstone interfaces. Light coloured "reduction spheres," so common in red beds of various ages elsewhere, occur occasionally in siltstones and claystones. Absence of reduction criteria in quantity indicates continuing maintenance of newly deposited red sediments above the water table long enough to permit destruction of most carbonaceous material by oxidation and aerobic bacterial action.

The main sedimentary features of the red beds are related to channel and floodplain phenomena; the coarser clastics and especially the clay breccias seem to be of scour and fill origin. What ripple mark is present in sandstones seems to be of current type, and interference ripples and "beach" cusps occur locally. Shallow lacustrine deposition might account for broad and regularly laminated silty sandstones evidently representing topset deposition. Except for the freshwater limestones and occasional shale bodies, I have seen no convincing evidence of paludal environments; most of the dark rocks near Gallows Point seem too coarse to be attributed to pond deposition. Coarser clastic bodies are very often broadly lenticular when seen in vertical (the principal available) outcrop. Finer sediments beneath such bodies extend laterally to the edges where the local unconformities disappear and the section continues upward until again interrupted by scour and fill.

Vertical repetition of the various lithologies is remarkable and may evince cyclical influences, though this is by no means certain. The occurrence of freshwater sharks (*Xenacanthus*) and aestivating dipnoans, total absence of molluscs and brachiopods, and all other features usually associated with marine deposition combine to suggest deposition under freshwater conditions.

Such characteristics bespeak a subaerial, aggrading, and fairly well-drained surface, most probably deltaic, on which large lakes developed only occasionally and for relatively brief periods of time. The repetition of scour and fill features and torrential clastics indicate that subaerial surfaces were subjected to periodic and short-lived flooding from near-by uplands. Drainage was largely confined to a few large channels whose adjacent floodplains were broad and relatively dry.

The scarcity of vertebrate fossils, seemingly reinforced by a lack of fossil plants, might suggest absence of favourable habitats. However, fossil vertebrates are never common throughout extended red bed sequences; their discovery in Palaeozoic and Mesozoic rocks is the exception rather than the rule. Absence of plant fossils in red beds is a fairly characteristic phenomenon resulting from destruction by chemical processes of most of the carbonaceous material buried in the sediments. The variety of reptiles in the small sample from Prince Edward Island shows, however, that this element of the fauna was diversified, and imperfection of the sample is attributable to unfavourable conditions for preservation, such as might occur on well-drained surfaces subjected to repeated sheet flooding. But relative abundance of reptiles in comparison to the numbers and varieties of amphibians and fish may imply a relatively dry environment. Absence of paludal deposits and the widespread occurrence of *Walchia*-type remains even in the red sandstones suggest a xeric environment. A suggestion of periodic, possibly seasonal, drying is to be found in the dipnoan burrow. This is *prima facie* evidence of aestivation, a habit unessential to fishes enjoying life in permanent bodies of water.

Interesting then is the general scarcity of desiccation features in the sediments. The few examples of mud crack I have seen are reflected in the lower surfaces of sandstones overlying silt and clay strata, but these are not of widespread occurrence. Nor are there many other sedimentary structures that would evince broad subaerial exposure: rain print, trails, swash, and rill marks are not common. This condition is perhaps explained by the fact that sudden sheet flooding of clay and silt desiccation surfaces would sweep up shallow mud cracks and incorporate them, more-or-less rolled and rounded in the clay breccias and conglomerates. Presence of very angular, tabular clay pellets supports this idea, and at one place near Crown Point I have observed mud curls preserved in sandstones.

What climatic significance is to be attached to the heavy calcareous induration of much of the clay breccia is unknown. There is no clear indication of evaporite deposits, suggesting, perhaps, that the delta lakes were drained rather than dried by evaporation.

A subsurface section revealed by drilling near Governor Island probably includes the complete Pictou (Upper Pennsylvanian) sequence (Milligan, 1949). Essentially red bed strata are reported to a depth of about 12,450 feet with only a few interruptions by thin coal stringers. No limestone is present above —12,450 feet (a thick salt deposit beneath this is probably intrusive). Submersion by marine waters therefore probably did not occur here during most of later Pennsylvanian time, but grey beds at intervals may indicate periods of relatively elevated water tables.

Whether any of the coals are autochthonous and reflect local swampy environments is not apparent from the data. The red beds exposed on Prince Edward Island are merely a continuation of the most recent sedimentation seen in this section and contain no coal or calcareous clay. Whether any regional unconformities occur in the section is uncertain. (Early writers reported some but did not agree on the positions of the breaks, and I believe they may have been confused by truncation of the unusually broad foreset laminae in some of the sandstones.)

The repetition of the lithological sequence detectable in the combined drill hole and surface sections suggests cyclical deposition, but the picture is not that of a classical cyclothem. Nor are the cycles so apparent as in the modified Dunkard cyclothem which also lack typical marine units (Beerbower, 1961). The impression is one of fairly uniform and regular subaerial deltaic deposition under relatively uniform climatic conditions for an extended period of time. Isostatic movements in the region of the delta apparently were maintained near equilibrium throughout late Stephanian and early Permian times. The site of deposition was relatively more elevated, and the climate was relatively drier than in the nearby, contemporaneous Dunkard deltas to the southwest.

RÉSUMÉ

Les roches sédimentaires rouges de l'île du Prince-Edouard ont rendu quelques fossiles. C'était un fait reconnu depuis près d'un siècle et quart que ces roches contenaient des vestiges de plantes et c'est en se fondant sur ces vestiges que nous avons attribué ces roches sédimentaires rouges aux périodes du Carbonifère, du Permien et du Trias. Jusqu'à ces derniers temps, nous ne connaissions que deux spécimens de fossiles de vertébrés, dont l'un était attribué à diverses espèces ayant vécu de la période stéphannienne au Trias. Des récentes découvertes ont ajouté plusieurs spécimens à la liste des vertébrés, y compris des formes étroitement apparentées à des genres trouvés dans les roches sédimentaires rouges de la période permienne dans le sud-ouest des Etats-Unis, ce qui porte à croire que ces roches remontent à peu près à la période léonardienne-wolfcampienne. Certains vestiges paléobotaniques militent en faveur de la présence de roches formées vers la fin du Pennsylvanien supérieur à divers endroits où les fossiles de vertébrés ne permettent aucune conclusion sûre. La présence de dépôts sédimentaires du Trias n'a pas été confirmée. Pour le moment, nous sommes portés à croire que les roches sédimentaires rouges sont plutôt d'origine permienne et permo-carbonifère.

L'ensemble des vertébrés connus de cette section stratigraphique est actuellement très limité. La diversité des reptiles et l'absence relative d'amphibiens et de poissons portent à croire à des milieux quelque peu plus secs que ceux qui existaient à peu près à la même époque dans la région des dépôts sédimentaires de Dunkard, au sud-ouest. La surface était peut-être mieux drainée que les deltas sur lesquels se formèrent les roches sédimentaires de Wichita et de Clear Fork, au Texas et dans le voisinage. Certaines caractéristiques sédimentaires de ces roches rouges semblent appuyer cette théorie. La présence d'un dipneuste passant en léthargie les mois d'été à la partie inférieure de la section stratigraphique nous fait supposer que le climat était nettement saisonnier au début de la période permienne.

ADDENDUM

While this paper was in press, a number of additional specimens were obtained from clay breccias in the Montague area by Dr. Larry Frankel. Of interest are several *Xenacanthus* teeth, better preserved than those described above. The specimens (NMC 10021 and 10022) have one or more cuspules and, though worn, show that heavy crenulations were present on the cusps. They are very similar to several *X. texensis* teeth at hand, from the upper Admiral formation in Texas. Apical buttons, however, seem less well developed on the teeth from Prince Edward Island. Two specimens are from surface blocks found in a field just north of the highway between Vernon and the Cherry Valley—Cherry Valley South road, a few hundred yards east of the intersection (Locality P-6202). Three other teeth are from shore-line exposures midway between Pownal and Cherry Valley (P-6201).

Also from this locality is the proximal end of a tibia (NMC 10019) referable to *Ophiacodon*. The specimen is within the size range of *O. retro-versus*, but the shaft is relatively slender. This bone bears a number of interesting punctures near the proximal end that may have been inflicted by some contemporary carnivorous animal—a *Xenacanthus* tooth was found in the matrix wedged against the articular surface of the tibia; the two others lay in matrix nearby!

Ophiacodon in the Prince Edward Island red beds is illuminating. The genus is essentially a Permian form and in Texas is apparently restricted to the Wichita group. The tibia lay adjacent to *Xenacanthus* teeth very comparable to the Wichita species and similar to *Xenacanthus* teeth from elsewhere on Prince Edward Island. This association provides somewhat stronger evidence that red beds along the south coast which are called Permo-Carboniferous in this paper should be assigned to the Permian system.

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